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## CORRESPONDENCE.

[Correspondents are requested to write briefly and to the point. No attention will be paid to anonymous communications.]

**The Evolution of the Colors of North American Land Birds.—A Reply to Criticism.**

TO THE EDITORS OF 'THE AUK':—

*Dear Sirs:* IN 'THE AUK' for April Mr. Allen takes occasion to review my recent paper, finding therein little to commend and much to condemn. Were his remarks mere statements of personal opinion I should not venture to question them, but as he has mentioned a number of passages confirming his opinions, it seems to me that they are worthy of a somewhat fuller discussion. It is generally held a just criterion of criticism to judge a writer by what he has professed to do rather than to blame him for not accomplishing what was not attempted, but this rule Mr. Allen seems to have disregarded. He does me the justice of quoting fully from the preface the intention of the paper, viz., to put forth a provisional explanation of the markings of birds supported by a greater or less number of facts, with the hope of awakening interest and stimulating research in a new field, but in the rest of his review treats this statement of my intentions as if it had no reference to the work in hand. [1] He seems to have little respect for speculative science, and condemns the philosophizing of Poulton, Romanes, and Weismann. It appears remarkable indeed that any scientist since the time of Darwin should be too narrow to see the value of such work. For example, Mr. Allen is a firm believer in the inheritance of acquired characters, and can he for a moment deny that the intense discussion of this subject incited by the researches and speculations of Weismann has given the world a far deeper and broader insight into this most intricate of questions? [2] There can be no doubt that the speculative method is open to great abuse when recklessly pushed in advance of empirical observation, but when coupled with this it becomes all important in the advance of real knowledge. Mr. Allen would have us progress only along such lines as we can absolutely establish for all time, but this is clearly impossible. Science like all other knowledge is a process of growth in which there is a continual selection of truth and an elimination of error. Let us by all means have an abundance of material to select from. Look at almost any scientific work of fifty years ago, and unless it treat of mathematics it will be found valueless, in large measure, at the present time, although its place may have been an important one as a stepping stone to something better.

But aside from general considerations, it is of some of his detailed criticisms that I wish to speak. Mr. Allen says without any reservation that my interpretation of the change of color in the young Arizona Hooded

Oriole is erroneous. He does not state why, as he says, "it is evident that this mottled phase of plumage, occurring in a very large number of species, is a permanent one for the time being . . .," but remarks that the assertion of a transition plumage "must be based on observation of the living bird for a sufficient period to determine the nature of the change of color." If this be so, then how can he so positively assert that the color does not change in the young Oriole? Has he observed this in the living bird? If so, he has forgotten to mention the fact, but if not, his own conclusion is of no more value than mine, according to the requirements he has himself made. However, as far back as 1835, as is noted in my paper, Yarrell recorded experiments of the sort demanded by Mr. Allen, to prove that in certain species there is a change in color without moult, viz., by marking feathers on living birds and observing the change. Mr. Witmer Stone writes me on this subject as follows: "I have been paying especial attention to young birds in first plumage during the past year, and while I cannot agree with Yarrell's idea of the plumage changing without moult as a general rule, I think that in some instances it is correct. In *Icterus spurius*, for instance, I cannot detect any moult from the first plumage to the fall dress of the 'bird of the year,' but there seems to be a darkening or intensification of the pigment." Dr. C. Hart Merriam and Dr. L. Stejneger have both asserted that in certain species a pigment change without moult occurs, and even if the old experiment of Yarrell, when applied to Orioles, should prove my deduction to be incorrect, it would not invalidate the assertion that in certain exceptional instances there is a change of color without moult. [3]

Concerning the mode of pigmentation of a feather, I would say that although in the text of my paper I have neglected to allude to the embryonic development of a feather, I am of course aware that the pigment is deposited during the process of formation of the feather. I am acquainted with what Burmeister, Owen, Wiedersheim, and others say about feather growth, but find nothing in their accounts to invalidate the position taken in my paper—viz., that the pigment is deposited along the lines of greatest and least resistance. Burmeister does not even allude to detecting pigment cells until the feather has attained a tolerably advanced stage of development. He says: "But, if the feather be colored, an accumulation of pigment is formed on each of the oblique striæ above each of its individual cells, and this is larger the nearer the cell is to the main stem of the barb."<sup>1</sup> This remark with others of a like nature would rather strengthen than detract from my contention that pigment deposition is in accordance with Prof. Cope's law of growth force.

The remarks upon hybrid feathers which Mr. Allen calls "the various classifications and generalizations based on this erroneous departure," are quite independent of the theory intended to account for them. It is merely an attempt to classify certain facts, which, so far as I can discover, have been previously ignored,—viz., the plan of coloration of individual feathers

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<sup>1</sup> Nitzsch's Pterylography, p. 8.

which in masses produce a definite color pattern. Mr. Allen's little exclamation about "the fewer facts for a nicely spun theory the better" is consequently not inserted in a suitable place, since I am not dealing with theories in this particular instance.

While Mr. Allen's objection that the pigment is deposited before the feather leaves the sheath does not interfere with my view of deposition along lines of greatest and least resistance, it may very seriously interfere with his own theory of climatic influences on color (which I have also accepted in my paper). Mr. Wallace writes me as follows on this subject: "There is a point you do not refer to which seems to me most important—that is, whether the colours and markings of the feathers are developed in the young feather before it has opened out of its sheath, as we know that all the markings of the wings of butterflies are to be seen before it emerges from the pupa. If it is so, then *climate can hardly have any direct influence*."<sup>1</sup> It is quite apparent that if Mr. Allen is not prepared to admit that some pigment is either deposited on or withdrawn from the fully formed feather, then climate can produce no effect on pigmental colors. It would thus seem as if he should at least be willing to share the humiliating mistake with which he charges me. [4]

In a foot-note he also alludes to a supposed new feather structure noted by me in 'Zoe,' and refers me to Coues's 'Key to North American Birds' for a description (p. 86). Following is the description there given: "*Filoplumes, filoplumæ*, or thread-feathers, have an extremely slender, almost invisible stem, not well distinguished into barrel and shaft, and usually no vane, *unless a terminal tuft of barbs may be held for such*." Upon referring to Nitzsch I found only two forms of filoplumes figured, both with the terminal tuft of barbs, and I consequently supposed the structure which I briefly and tentatively recorded as having no barbs whatever, was different. Upon further examination of the text of Nitzsch I find he has included this form also under the head of filopluma, without, however, figuring it in the plate.

Mr. Allen is also quite right in saying that I have been handicapped in my work by insufficient knowledge of exotic birds, my opportunities for studying these having been very limited upon the Pacific Coast where no satisfactory collections are available. In speaking of patterns of marking with which I am unfamiliar, I had no intention of asserting that such did not exist, but simply that they were quite unusual if they did occur among North American species, whereas other forms are very often repeated. Exceptions (even a considerable number of them in fact) would not invalidate the conclusions so long as a fair ratio was maintained between the unusual forms and the most common styles.

Mr. Allen must have taken especial pains to discover a contradiction where none exists in referring to the Brown Creeper, in order to bring in his phrase of "slipshod generalization." [5] It would seem as if in a paper

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<sup>1</sup> Italics mine.

where so many generalizations are made he could have been more judicious in selecting an example to fit the term. In speaking of color determining habit I referred only to the general shade of color—brown genera would be forced by natural selection to the ground and olive-green birds to the trees; but in speaking of the Brown Creeper I refer to its detailed markings and streaks, in which we have not a perfect illustration, but “the nearest approach” to an instance of special protective resemblance.

In speaking of the Passenger Pigeon Mr. Allen takes the trouble to italicize the assertion that the tail markings to which I allude as recognition marks “are found only at the extreme base of the tail, within the area normally concealed by the coverts, *and are therefore not visible under any ordinary conditions.*” If he will take the trouble, instead of merely looking at a skin with closed tail, to *spread the tail feathers*, as a bird does at every turn in its evolutions, he will find a conspicuous broad band of dark brown strongly relieved against the white of the under tail-coverts and contrasted also with the conspicuous white outer tail-feathers. Although I have seen the Passenger Pigeon alive I do not now remember how distinctly the tail markings showed, but I have in no instance in the text of my paper implied that the conclusions were based upon the study of live birds, except in certain instances where this was stated. [6] Slips in nomenclature are never pardonable in a work of this sort, but by way of explanation I may state that I was suffering from an attack of nervous prostration during the publication of the latter part of the work, and was physically unable to give it the care which it demanded.

Mr. Allen fails to see any use in the plate showing the evolution of the pattern of head markings, since, as I have said in the text, the relationships “are not supposed to be genetic.” The plate is intended to show that among living North American birds various types of head markings exist which are related more or less nearly to one or all of the five types with simple longitudinal streaks. There is no way in which we can now learn the colors of extinct birds, and it is consequently entirely out of the question to think of presenting a genetic series of head markings to show their evolutionary sequence. The most that can be done is to show that living birds happen to represent different stages in an ideal sequence from a streaked plumage, and this taken in connection with the fact that the streaked feather is the elementary type of feather marking, [7] and with the *a priori* considerations as to why it should be so, serves to confirm, without necessarily proving, the supposition that the head markings have all been evolved from longitudinal streaks.

The fact that in comparing low groups of birds like the Pigeons and Tinamous with such high groups as the Thrushes and Sparrows the latter are found to have a streaked plumage where the former have not, is in no wise contradictory to the assertion that the streaked plumage is the primitive type. Surely no one ever made the absurd assertion that color development advanced from the lowest to the highest groups of birds *pari passu* with structural development. How then could we explain the high development of markings in Auklets and Ducks, and the brilliant plumage

of Pigeons? Many large groups have become highly specialized on a low type of organization, and show a far more complicated color development than the highest families in the scale.

In a review as long as that of Mr. Allen, it would have seemed reasonable to expect that he would have found room for at least a bare mention of the most important suggestions in the paper in question. Although he alludes to the "large amount of nonsense" in the discussion of recognition markings in which I have simply elaborated some of the views of Wallace and Poulton, following directly in their footsteps, he does not even mention the law of the assortment of pigments, which Prof. Cope considers the most important original contribution of the paper, [8] nor to numerous other matters of greatly more importance than the tail markings of the Passenger Pigeon. I am well aware that the paper is open to an unlimited amount of criticism, but as I asserted in the preface it was not written with any idea of being final or conclusive, but simply to stimulate thought in a new line and to awaken more competent investigators to a new field of research. If it accomplish this I am quite willing to see it overwhelmed with criticism and die, but I appeal to the ornithologists of America not to let it die without bearing some little fruit. Whatever the critics may say I am convinced that amongst the mass of rubbish, if such it be, there are some few suggestions that will be of value in the elucidation of the problems of color evolution, and I most ardently hope that they will be sought out and developed into something better and more worthy of lasting.

CHARLES A. KEELER.

*Berkeley, Cal., Sept. 11, 1893.*

[Having given Mr. Keeler so much space, my reply must be as brief as possible, and might be much shorter than it is had Mr. Keeler been a little more exact in his statements as to what I really said in my review of his work. To save space I have inserted numbers enclosed in brackets after the points which seem most to require notice, and reply to them in the correspondingly numbered paragraphs which follow.

1. In fact, Mr. Keeler himself seems to have forgotten this modest and tentative attitude throughout the greater part of his work.

2. What I really said on this point needs no qualification, namely, that "much of the speculative writings of Poulton, Romanes, Weismann, and many other writers who have of late been so prolific of explanations of the abstruse things in nature" is natural history romancing posing as science. This is not a general condemnation of the scientific work of these writers, for it is far from my desire to deny to either of them, and particularly to Weismann, the credit of contributing, through genuine research, to the real progress of science. Neither did I so thoroughly condemn Mr. Keeler's own work as his opening sentences above imply; "on the contrary," to quote from my review, "we find much to commend in Mr. Keeler" (p. 190); and again: "In the two hundred and odd pages

devoted to the 'Colors of North American Birds' there is much that is suggestive and worthy of commendation, mixed with a great deal that is weak and unphilosophical," etc. (p. 191). Or again: "While there is much that is valuable in the work, and many points that are well taken, Part II especially is largely vitiated by unsound reasoning, by misapprehension of facts, or by lack of general information on special points" (p. 194). The trouble is that Mr. Keeler seems unable to distinguish between pure speculation and reasonable hypothesis.

3. It is not claimed that there is never any change in the color of feathers without a moult, aside from the fading and very pronounced change we know to take place simply by exposure of the plumage to the elements. The case of the Oriole simply typifies a large class of cases where there is a transitional, immature dress characteristic for a season or two, according to the species, of the young male in a great many kinds of birds. The evidence, not altogether negative, that this is what it seems, and is generally believed to be, namely, a true transition stage, where often it is difficult to find two birds marked exactly alike, is so overwhelming and conclusive that the *onus probandi* fairly rests on the supporters of the opposing theory that the birds are gradually acquiring the perfect or adult plumage by a radical, gradual change of color in the mature feather *without* moult. To recite the evidence against this kind of change would require far more space than can here be spared.<sup>1</sup> In this connection, however, it may be noted that a microscopical examination of the mature feathers of Orioles, which Mr. Keeler assumes gradually change from olive to black, will probably show that pigment has very little to do with the case. Should such prove to be the fact the question could be readily settled; for it seems too much to suppose that there can be sufficient structural or molecular change in the mature feather to produce a radical change of color.

4. This is a postulate I am surprised to see emanate from Mr. Wallace, or even Mr. Keeler! It is true that we know little of the *method* of physiological action resulting from climatic influences, but the *results* of this potent force, encountered on every hand, are too evident to be overlooked. That humidity, or its absence, acts directly on the fully formed feather so as to cause the "*deposit*," or "*withdrawal*," of pigment is a conception too absurd for serious consideration, beyond the obvious fact that feathers do fade through exposure, in the living bird as well as in the museum specimen, somewhat in ratio to the degree of aridity and the intensity of the bleaching sunlight to which they are exposed. But the gradual evolution of a permanent change of color, such as marks geographical races or representative species for example, must obviously be due to the long-continued action of the environing conditions upon the

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<sup>1</sup> See some remarks on this point, however, in Bull. Am. Mus. Nat. Hist., Vol. V, p. 108.

whole organism, and thus involving, among other changes, the amount and character of the pigment *at the time of its deposition during the formative stage of the feather.*

5. Any fair-minded reader who will take the trouble to see how the phrase "slipshod generalization" is introduced will see that it has no necessary bearing on the case of the Brown Creeper, but relates directly to his assumption that "the habits of birds have been more or less determined by their colors," and to his explanation of how they have been so determined. In case there is any connection between color and habits, it is habit that has determined color, according to the views of most evolutionists, rather than color that has determined habit, which seems to be purely a discovery of Mr. Keeler's.

6. When Mr. Keeler has observed the living bird and found that when the Pigeon spreads its tail it spreads only the rectrices and not the lower coverts as well, it will be time to consider the point made in his rejoinder as well taken.

7. It is perhaps worth while to state that "the *fact* that the streaked feather is the elementary type of feather marking" is not accepted as a "fact" to the extent Mr. Keeler's positive statement might lead one to suppose. Indeed, the opinion of several eminent investigators who have recently expressed themselves on the subject is quite the reverse, both Kerschner and Gadow, for example, believing that the distribution of coloring matter in *transverse bars and lines* is phylogenetically the older method.

8. Professor Cope, in reviewing Mr. Keeler's work in the 'American Naturalist' (June, 1893, p. 459) has said: "The most important contribution towards the discovery of the origin of colors in birds by Mr. Keeler is his *demonstration*<sup>1</sup> of the law of the Assortment of Pigments. His classification of our birds in accordance with their color relations, is a valuable preliminary to further research." But it is impossible for me to believe that Professor Cope spoke from a due consideration of the subject or from any intimate knowledge of the facts involved. His careless mention of the matter is evident from his reference to Mr. Keeler's "demonstration" of his law, when Mr. Keeler tentatively puts it forth with the usual 'ifs' and other qualifications, and says distinctly that the "theory could not be demonstrated without further study of the chemical properties of pigment"; and further adds: "Until such experiments have been made, however, it is necessary to depend upon appearances, and here there are many facts that seem to support the view." This, then, is Professor Cope's "demonstration" of "the law of the assortment of pigments," which seems to give Mr. Keeler so much consolation.

It is needless to say that I look upon this theory as no better than numerous others I took the trouble to criticise, and almost regret that I am now called upon to expose its worthlessness. It is based on pure

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<sup>1</sup>Italics mine.



guess-work, with no basis in experiment, microscopical study, chemical analysis, or properly observed facts of any sort, as shown by Mr. Keeler's own statements. He is speaking, or supposes he is speaking, of pigment, but his remarks show that he refers to color in a broad sense. Yet no blue pigment has ever been discovered, and green and yellow are well-known to be not by any means always due to pigment, but are merely 'objective structural colors.' Thus, according to Gadow, violet and blue always belong to this category, green almost always, and yellow occasionally. And among the instances he cites where "yellow feathers are in reality without pigment" are such birds as *Icterus* (!), *Xanthomelas*, *Picus*, etc. Green, except in the Musophagidæ, "is always due to yellow, orange, or grayish brown pigment with a special superstructure, which consists either of narrow longitudinal ridges, . . . or else . . . the surface of the rami and radii is smooth and quite transparent, while between it and the pigment exists a layer of small polygonal bodies, similar to those of blue feathers." Further space cannot be given to the subject in this connection, but the reader is advised to carefully study, in connection with Mr. Keeler's "theory of the assortment of pigments," and related parts of his work, the article on 'Colour' by Dr. Hans Gadow in Professor Newton's recently published 'Dictionary of Birds,' from which some of the above statements are quoted.

It is evident that if Mr. Keeler had possessed what may be termed even a fair superficial knowledge of the investigations that have been made respecting pigments, and the structure of feathers in relation to color, he could not have propounded so utterly defenceless a hypothesis as his "Law of the Assortment of Pigments," and would have omitted a great deal of the "rubbish" that he has put into his book on the general subject of the "evolution of colors" in birds.

Many of the minor points in Mr. Keeler's rejoinder are passed over as hardly demanding space for formal consideration, even though the real bearing of my criticisms is in several instances greatly misrepresented.

In conclusion I may add that the task of reviewing Mr. Keeler's book was a painful one, and was prompted only by a sense of duty, not only to the many inexperienced readers who might be misled by it, but as a needed protest against a very prevalent kind of pseudo-science that has of late gained great currency and popularity. That some such antidote was not wholly unnecessary is shown by the fact that the editor of a prominent scientific journal is found to have endorsed one of its most groundless hypotheses.—J. A. ALLEN.]

### Birds of British Columbia and Washington.

TO THE EDITORS OF THE AUK:—

*Dear Sirs:*—Over the initials "C. F. B." there appeared in the last number of 'The Auk' a review of my final paper on the Birds of British Columbia and Washington.